

# THE ORIGIN OF THE INFLORESCENCES OF XANTHIUM

CLIFFORD H. FARR

(WITH PLATE X)

The bur of *Xanthium*, together with the two inclosed seeds, has been the subject of considerable investigation for many years. ARTHUR (1) in 1895 confirmed the popular notion that the germination of one of the seeds is delayed approximately a year beyond the other, and also that it is the lower and better developed seed which germinates first. CROCKER'S experiments (5) in 1906 indicated that this phenomenon is due to a difference in the permeability of the seed coats to oxygen. In 1911 SHULL (14) demonstrated further that the embryos differ in the amount of oxygen required for germination; and the same writer (15) has published an article more recently on the nature of the semipermeability of the seed coats. In addition to these physiological studies, the structure of the seed coats has been investigated by HANAUSEK (10).

The morphology of the pistillate inflorescence, or bur, has been much discussed and variously interpreted. The oldest and most generally accepted view is that which considers it a fusion of involucreal bracts. This was supported by WARMING (16) and ROSTOWZEW (13), and accepted by ARTHUR, GRAY, and BRITTON. As early as 1838 BRASSAI (3) dissented from this interpretation and referred to the bur as a fusion of many floral bracts. Later BAILLON (2) modified BRASSAI'S idea by assuming a union of but two floral bracts, coalesced along their margins; and GOEBEL in his most recent paper (9) accepts this explanation. However, only three years before, the last named writer (8) presented another possibility, namely, an intercalary growth about the base of the flowers, enveloping them and carrying their floral bracts upward to form the beaks.

There is also a marked difference of opinion as to the morphology of the spines which are so prominent on the mature bur. CLOS (4) suggested that these are new structures ("Emergenzen"),

and he has been followed in this by many workers, including BAILLON (2) and GOEBEL (9). However, KOEHNE (12) as long ago as 1869 conceived of them as involucre bracts; while HOFMANN (6) referred to them as "Spreublätter"; and ROSTOWZEW (13) simply called them modified bracts.

These diversities of interpretation have doubtless been due to an inadequate knowledge of organogeny, and to an incomplete correlation of the spines, bracts, etc., of related genera. A considerable number of typical Compositae have been investigated and the morphology of their parts is well established. The Ambrosiaceae, the tribe to which *Xanthium* belongs, has been excluded from the Compositae by some, though several of its genera approach very near to the typical form of Compositae. *Iva* is without doubt that member of the Ambrosiaceae most closely resembling these Compositae, and a recent discussion of *Iva xanthiifolia* Nutt. by the writer (7) involved the homology of its bracts and rudimentary structures with corresponding organs in the inflorescence of the typical Compositae. This paper also presented a hypothesis as to the origin of dicliny in that species. The present investigation was undertaken in the hope that the results of the preceding study might aid in the explanation of the dicliny in *Xanthium* and the interpretation of its peculiar pistillate inflorescence. I wish to express my appreciation for the encouragement and suggestions of Dr. R. B. WYLIE under whose supervision the work was pursued; and thanks are also due to Dr. J. C. ARTHUR for assistance in the determination of species.

### The staminate inflorescence

The species investigated was *Xanthium commune* Britton, in which staminate and pistillate capitula are associated on the same branch. The staminate head, which bears 150–175 flowers, is often solitary and always terminal, thus occupying an exposed position. The peduncle (fig. 2) on which it rises above the pistillate heads is quite slender in comparison with similar structures. Its length nearly always equals or exceeds the diameter of the head which it bears; while its own diameter is only about one-sixth as great. Three vascular bundles (fig. 4) run throughout the length of the peduncle,

and the vestiges of three others appear in its lower portion (fig. 3). These vestiges suggest that the peduncle of the staminate head once possessed a more extensive vascular system. This conclusion is further supported by the larger number of bundles in the base of the pistillate head. GOEBEL (9), in explaining the existence of the two or three bundles in the peduncle of the staminate head of *Ambrosia*, made use of a similar hypothesis of reduction, though he presented neither of the above lines of evidence. In *Xanthium* we find that now only three bundles conduct all the water for 150 or more staminate flowers. This supply seems all the more meager when it is noted how scantily this head is protected against water loss. Only a few involucre bracts mature, and these are so small as to be of scarcely any service to the capitulum in its older stages.

The conical receptacle (fig. 1), when young, so closely resembles a developing spike that WARMING'S generally accepted theory as to the spicate origin of the capitulum is at once recalled. As in most Compositae, the marginal flowers appear first, and the apical region maintains its meristematic nature for some time. Each flower is subtended by a cylindrical or spinelike floral bract which, though furnishing slight protection, probably does not appreciably lessen the amount of transpiration.

The parts of the flower appear in centripetal order. A lobed corolla is followed by a whorl of four or five stamens, and finally a pair of carpels. About one-third to one-half of the flowers in each head have only four stamens, not even the rudiment of a fifth appearing. In flowers with five stamens the corolla always possesses five equal lobes. In those with four stamens the corolla may have either four equal or five unequal lobes. In the last case two lobes frequently represent quadrants, while the other three make up the remainder of the cycle. Evidently the primitive staminate flower of *Xanthium* was pentamerous with respect to petals and stamens. It follows, therefore, that in some cases a reduction has taken place in the number of stamens and corolla lobes, the former yielding more readily than the latter.

The stamens are always united by their filaments. Though ROSTOWZEW (13) and JUEL (11) report that the anthers never fuse, in *Xanthium commune* the adjacent anthers are sometimes joined

in the same manner as in *Iva* (7). The fused cutinized layer is, however, not quite as thick as in the latter form. The similarity between *Xanthium* and *Iva* further extends to the ringlike enlargement at the base of the abortive style. These facts only serve to emphasize the kinship of these two genera with the main body of the Compositae.

ROSTOWZEW (13) stated that the stigma of the abortive style probably does not represent two carpels. In *Iva*, though this abortive stigma is not bifid at maturity, the appearance of a notch at the apex during development indicates derivation from the typical bifid form. Since no such notch appears in *Xanthium*, it seems probable that this genus has gone one step farther and obliterated even this last clue to the evolution of this structure. The close relationship of this form of *Iva*, however, strongly suggests that this rudimentary style arose from the usual bifid form.

### The pistillate inflorescence

The fertile flower is axillary, being subtended (figs. 4-6) by a leaf or another pistillate head. Many instances of aborting leaves in such relation explain the frequent absence of subtending structures at maturity. The nearly sessile capitulum is attached to the floral axis by a large base which is over twice the diameter of the peduncle of the staminate head and contains 24 bundles (fig. 5). This vascular supply, in contrast to that of the staminate head, seems remarkably extensive when it is recalled that the pistillate head bears only two flowers, while the staminate has 150 or more.

The involucrel bracts, 9-15 in number, appear first and arch over the young head, protecting it very effectively. The proximal ends of the adaxial bracts are closely crowded between the receptacle and the stem, and those on the abaxial side between the receptacle and the subtending structure. Meanwhile the tips of these recurved bracts (fig. 6) come in touch with the apex of the growing receptacle near its center. It seems that this contact temporarily arrests development in that region of the receptacle, for it immediately becomes flattened. Soon continued growth of the margin of the receptacle results in the formation of an apical depression (fig. 7). It may be, of course, that this sequence of

events has become fixed in the life-history, but arrest of development in the center of the receptacle due to contact with the apices of the involucre bracts might explain its origin both in individual and racial development. In the light of the foregoing it is evident that the terminal heads develop as in the normal Compositae, because the involucre bracts are not hemmed in by subtending structures and hence their tips probably do not come in contact with the receptacle.

Growth in the marginal region is lateral as well as longitudinal, making the depression larger at the bottom and constricted above. Furthermore, the floor of the pit is never a uniformly concave surface, but is slightly elevated at its exact center (fig. 7). This elevation soon resumes growth (fig. 8) and gives rise to a septum dividing the depression into two chambers (fig. 9). Later this septum develops in its upper surface a cleft which may extend downward some distance (fig. 13).

Many papillae early cover the marginal surface of the receptacle (figs. 8 and 9), as in the staminate head. Those of the latter, it will be recalled, give rise to the flowers and floral bracts, while these papillae of the pistillate head form hard hooked spines (fig. 13). That these spines are homologous with the floral bracts of the staminate head seems reasonably certain. It is hardly likely that flowers would become transformed into such structures by any process of evolution. These spines have the form and spiral arrangement of floral bracts. Furthermore, ROSTOWZEW (13) has shown that the vascular anatomy is like that of bracts. To consider them new structures would be to assume the disappearance of floral bracts and the subsequent appearance of structures similar to them in exactly the same location. Such a substitution is not supported by the observed facts. It seems, therefore, that there is abundant evidence for considering these structures floral bracts.

The margin of the head grows more rapidly on one side, causing one of the depressions to become deeper. This unequal growth also accounts for the peculiarity noted by ARTHUR (1) that the bur is flat on one side and curved on the other. The two flowers appear simultaneously, one at the bottom of each pit (fig. 8); but the lower, being in the deeper depression, is always larger, grows more rapidly, and at all stages of development is

more advanced than the upper. This difference persists even after fertilization, and in every case the lower seed bears the larger embryo. It is evident that the lower flower is in closer connection with the vascular supply, and possibly this circumstance, together with its priority in development, may have made a difference in the nutrition and water relations of the two flowers. These factors doubtless condition to a large extent the structure and composition of the seed coats and embryo, which in turn have been shown to influence germination. It thus appears that a difference in the rate of growth of the two sides of the young head and consequently the vertical displacement of one of the seeds results ultimately in a difference in the periods of delayed germination.

The sequence of development is the same for both flowers in the bur. The abortive corolla forms at first a complete ring (fig. 10), but before maturity it disappears entirely on the outer side (fig. 11). The two carpels, though appearing later, grow more rapidly than the corolla (fig. 10), and produce the bifid stigma which projects through the beaks at the time of pollination. One instance was noted in which two collar-like structures were present, the inner reaching but half-way around the base of the style. The outer, being a complete ring, is unquestionably the normal rudimentary corolla, and the inner should doubtless be considered the vestige of an abortive whorl of stamens, such as regularly appears in *Iva* (7).

A small rudiment of a floral bract is usually noticeable on the outer side of the base of the pistillate flower (fig. 12). It will be recalled that these flowers arise in deep cavities, the walls of which crowd closely about them on all sides. There is scarcely any space for the development of a floral bract therefore, and probably this crowding accounts for its reduction to the present dwarfed condition. Its presence, nevertheless, even though much reduced, precludes the possibility of considering the beaks to be the floral bracts of the subtended flowers.

### Discussion

If the bur of *Xanthium* in its individual development follows at all closely the course of its evolution, there seems no doubt of its being a modified capitulum. The involucre bracts arise in the

usual way; the floral bracts all develop into spines except those of the two inclosed flowers, which remain rudimentary; and the "Anlagen" of the two flowers which appear follow the normal sequence of development. The only respects in which this head differs from those of the typical Compositae are seen in the two beaks and the depressions which they subtend. The beaks cannot be considered as floral bracts of the subtended flowers, because the rudiments of these parts are present in the pits. Neither is it likely that they are the floral bracts of aborted flowers, for they are quite unlike the spines in form, structure, and development. The fact that they bear the spinelike floral bracts on their outer surfaces precludes their being interpreted as modified involucre bracts. Moreover, two whorls of involucre bracts have never been established for any of the Ambrosiaceae. Though some writers (13) have interpreted *Iva* as having a double whorl of involucre bracts, my study (7) has shown that the inner of these whorls might properly be regarded as the floral bracts of the pistillate flowers. It seems most reasonable, therefore, to interpret the beaks of *Xanthium*, not as modified bracts nor even as newly developed structures, but as portions of the receptacle formed by its upward growth, and slightly altered by proximity to the depressions. Under this interpretation the only modification required to transform a typical head of Compositae into a *Xanthium*-like bur is the formation of two depressions in the apical region. In this species it seems that these depressions arose, not by a sinking of the flowers into the receptacle as HOFMANN (6) suggests, nor by an intercalary growth in the surrounding regions, but rather by an arrest of development in the apex due possibly to contact with the tips of the involucre bracts at an early stage.

In a recent treatise on sexual differentiation in plants (8) GOEBEL ascribes to modifications of nutrition, not only the origin and evolution of sex, but all the phenomena of hermaphroditism, dicliny, and dioecism. He surveys the entire plant kingdom and applies his interpretation to both cryptogams and phanerogams, and to gametophyte and to sporophyte alike. Numerous experiments and observations indicate that in many cases nutrition does determine the sex of an individual or part. But, especially in the

higher plants, it is by no means certain that this is the only conditioning factor, and in some instances it seems to influence sexuality only remotely, if at all. An illustration of this last condition is found in *Iva xanthiifolia* (7). In it the staminate flowers seem to have been evolved by an abortion of the pistils, probably on account of exposure to excessive transpiration. On the other hand, the pistillate flowers appear to have arisen by an abortion of the stamens, brought about evidently through pressure on the terminal portion of the flower and consequently lack of space in which to develop. That such transitions could take place is evidenced by the fact that, a priori, stamens are better fitted both in structure and in function to endure desiccation than are pistils; while carpels, owing to their central (and in an epigynous flower, basal) position, are less susceptible to pressure and crowding.

*Xanthium*, a form with pistillate and staminate flowers in different heads, affords even stronger evidence in favor of this interpretation. In many respects the staminate flowers are more exposed to factors accelerating transpiration than are the pistillate. The staminate heads are terminal, peduncled, and not subtended by protecting leaves. Each is composed of 150 or more flowers, and is supplied by only three vascular bundles. Moreover, the flowers are borne on a highly convex receptacle, and are protected by only a few relatively small involucre bracts, while their floral bracts are mere spines. Since all these conditions are in marked contrast with those under which the pistillate flowers develop, it seems reasonable to conclude that abortion of pistils in flowers of terminal heads was due to lack of a water supply adequate for the high rate of transpiration.

On the other hand, the pistillate flowers are obviously subjected to greater lateral pressure and have only a limited space in which to develop. They occur in pits which are constricted at their openings, and are enveloped by a dense spine-covered bur. Furthermore, there is a mutual reduction of all floral appendages, including corolla, stamens, and floral bract, indicating that this abortion is due to an external cause. It seems probable, therefore, that the arrest of development in the stamens, and hence the derivation of

the pistillate flower, is a direct consequence of crowded conditions during growth.

The differences between the staminate and pistillate flowers with respect to their protection, vascular supply, and number per inflorescence have been variously interpreted. They have been considered either as secondary sexual characters, or as a direct consequence of the difference in sexuality. In the former case the characters associated with the pistillate inflorescence would be thought of as having no essential relation to the nature or function of the female sex. In the second case it would be held that the pistillate flower is protected because it is in need of protection. It is apparent that my interpretation follows neither the incidental nor the teleological views above named, but ascribes to the characters associated with each kind of flower a rôle of primary importance *in effecting* the transition from hermaphroditism to dicliny. In other words, many of the differences between pistillate and staminate flowers appeared while the flowers were still perfect; and the effects of their presence occasioned the abortion of pistils and stamens respectively, resulting in the dicliny of this species.

*Ambrosia* and *Franseria* resemble *Xanthium* not only in their type of dicliny, but also in the peculiar burlike female inflorescence, the principal difference being that they have but one flower in each pistillate capitulum. Although there is need of further investigation, it may be well at this time to note what relation these genera bear to the conclusions reached above. ROSTOWZEW (13) stated that the pistillate heads of both forms are found in the axils of leaves. Furthermore, GOEBEL (9), in referring to *Ambrosia*, said, "In no instance have I observed in the male capitula even a trace of a subtending bract." The vascular supply has been studied only in the peduncle of the staminate head of *Ambrosia*, in which the last named writer found only two or three bundles. It is a matter of common knowledge that in both these genera staminate heads are terminal and peduncled, while pistillate are axillary and sessile. Evidently, therefore, *Ambrosia* and *Franseria* agree closely with the conditions in *Xanthium* as regards the position, protection, and, so far as known, the vascular supply of the heads. Thus it seems likely that the foregoing interpretation of the origin

of dicliny and of the peculiar fertile inflorescence may prove applicable to other genera of the Ambrosiaceae.

### Summary and conclusions

1. The pistillate and staminate heads of *Xanthium commune* may be contrasted with respect to the following characters: position, attachment, subtending structures, number of involucre bracts, number of vascular bundles in the peduncle, number of flowers, and form of receptacle.

2. The pistillate and staminate flowers differ in degree of development of pistil, corolla, and floral bract. The stamens completely abort in the pistillate flower.

3. The vascular system in the peduncle of the staminate head has doubtless undergone reduction in the number of bundles.

4. The number of stamens per staminate flower is probably now undergoing reduction.

5. The anthers occasionally fuse, indicating relationship to the typical Compositae.

6. The bur is a modified capitulum, differing from the typical head of Compositae chiefly in the two depressions in the receptacle. These pits originate through a temporary arrest of development, which may possibly be attributed to contact with the tips of the recurved involucre bracts. This recurving of the bracts may be the result of limited space due to the subtending structures.

7. The spines of the bur are probably modified floral bracts.

8. The beaks seem to be modified portions of the receptacle.

9. The terminal heads became staminate, because the vascular supply was inadequate to compensate for the excessive transpiration, and hence the pistils have aborted.

10. The axillary heads became pistillate by the abortion of stamens, owing to the pressure and crowding incident to the formation of the flowers in depressions.

11. Many of the characters in which the pistillate and staminate flowers of *Xanthium* differ have been causative factors in the origin and development of dicliny in this form.

NOTE.—Since submitting the above for publication there has appeared an extensive study of abortive stamens by CURT SCHWARZE.<sup>1</sup> The author does not discuss the Compositae in this connection at all, nor does he refer to any recent work on that group. On the whole it presents very interesting corroborative evidence bearing on the conclusions reached above, when properly interpreted. Dr. SCHWARZE calls attention to SCHUMANN (1890) as the originator of the theory that reduction of stamens comes about through mutual external pressure of the organs in the bud. As opposed to this, he presents the contentions of FAMILLER (1896), MUTH, and others that abortion is due to internal factors, and himself suggests that these internal factors are constitutional in the protoplasm. This internal causation hypothesis is based on the failure in some cases to observe the parts in actual contact during development. It is evident that this is a very difficult point to demonstrate, as it necessarily involves disturbing the organs, which may itself separate surfaces loosely in contact. Moreover, recent investigations have served to greatly emphasize the delicacy of the sensitivity of plants to contact stimuli. But even granted that contact does not occur during the ontogeny of certain forms, there is still no reason that SCHUMANN and FAMILLER may not both have a correct interpretation. If we presume that the contact and mutual pressure did occur during the ontogeny of the ancestors of the living forms, such as is at present so striking in the Ambrosiaceae discussed above, it may be properly concluded with SCHUMANN that the pressure did cause an abortion. Such a reduction in size and arrest of development at an immature stage would necessarily involve a reduced vascular supply. Such a condition would doubtless result in diverted nutrition and water supply, which after many generations might make development of the stamens to maturity impossible even in the absence of mutual pressure. Thus by the reduced vascular supply becoming hereditarily fixed, there would be an internal cause for the abortion of the stamens, traceable to an original external condition. That the vascular supply is thus

<sup>1</sup> SCHWARZE, CURT, Vergleichende Entwicklungsgeschichtliche und histologische Untersuchungen reduzierter Staubblätter. *Jahrb. Wiss. Bot.* 54:183-243. 1914.

modified is indicated by the observations of SCHWARZE, in that the cells of abortive stamens are often more vacuolate than those of stamens developing to maturity.

#### LITERATURE CITED

1. ARTHUR, J. C., Delayed germination in cocklebur. Proc. Soc. Promotion Agric. Sci. 16th Ann. Meet. pp. 70-79. March 1896.
2. BAILLON, H., Organogénie des *Xanthium*. Adansonia 1:117. 1860.
3. BRASSAI, S., Flora oder Allg. Bot. Zeit. 21:308-310. 1838.
4. CLOS, D., De la signification des épines et des receptacles des fleurs femelles chez les *Xanthium*. Mém. Acad. Toulouse IV. 6:66-75. 1856.
5. CROCKER, WM., Rôle of seed coats in delayed germination. BOT. GAZ. 42:265-291. 1906.
6. ENGLER, A., and PRANTL, K., Die natürlichen Pflanzenfamilien. 4<sup>s</sup>:110. 1897.
7. FARR, C. H., The diclinous flowers of *Iva xanthiifolia* Nutt. Proc. Iowa Acad. Sci. 20:151-160. 1913.
8. GOEBEL, K., Über sexual Diphormismus bei Pflanzen. Biol. Centralbl. 30:656-678, 693-718, 721-737. 1910.
9. ———, Morphological notes. I: The inflorescences of the Ambrosiaceae. Proc. and Trans. Bot. Soc. Edinburgh 26:60-68. 1913.
10. HANAUSEK, T. F., Die Kohlenschichte in Kompositen Perikarp. Sitz. Kais. Acad. Wiss. Wien 116:3-32. 1907.
11. JUEL, C., Om pollinationsapparaten hos familjen Compositae. Svensk. Bot. Tidskr. 24:350-363. 1908.
12. KOEHNE, E., Über Bluthenentwicklung bei den Compositen. Dissert. Berlin. 1869.
13. ROSTOWZEW, S., Die Entwicklung der Bluthe und des Bluthenstandes bei einiger Arten der Gruppe Ambrosieae und Stellung der letzteren in System. Bibl. Bot. 4: 1890.
14. SHULL, C. A., The oxygen minimum and germination in *Xanthium* seeds. BOT. GAZ. 52:453-477. 1911.
15. ———, Semipermeability of seed coats. BOT. GAZ. 56:169-199. 1913.
16. WARMING, E., Die Blumen der Compositen. Hanstein Bot. Abhand. 3: 1876.

#### EXPLANATION OF PLATE X

The figures were made with a camera lucida. The magnifications given are those of the drawings before being reduced one-half in reproduction. The abbreviations used are as follows: *b*, beaks; *s*, spines; *i*, involucre bracts; *f*, floral bracts; *a*, abortive corolla; *r*, rudimentary floral bract; *p*, pistillate head; *c*, carpels; *l*, leaf; *w*, pistillate flower.

FIG. 1.—Apex of floral axis, showing a staminate head with two pistillate heads appearing at its base;  $\times 63$ .

FIG. 2.—Developing staminate head;  $\times 63$ .

FIG. 3.—Transverse section of lower end of peduncle of staminate head;  $\times 70$ .

FIG. 4.—Transverse section of upper end of peduncle of staminate head;  $\times 90$ .

FIG. 5.—Young pistillate head, showing recurved bract;  $\times 80$ .

FIG. 6.—Young pistillate head, slightly older;  $\times 80$ .

FIG. 7.—Young pistillate head, showing developing depression;  $\times 120$ .

FIG. 8.—Young pistillate head, showing flowers appearing in the pits;  $\times 85$ .

FIG. 9.—Transverse section of pistillate head with flowers partly developed;  $\times 90$ .

FIG. 10.—Young pistillate flower, with carpels appearing;  $\times 70$ .

FIG. 11.—Young pistillate flower from lower pit of same head as in fig. 10;  $\times 70$ .

FIG. 12.—Young pistillate flower, showing ovule appearing;  $\times 90$ .

FIG. 13.—Young pistillate flower from lower pit of same head as in fig. 12;  $\times 90$ .

FIG. 14.—Pistillate head at megaspore mother cell stage;  $\times 16$ .

FIG. 15.—Transverse section of base of pistillate head, showing bundles;  $\times 70$ .